

GROWTH STUDIES IN FOREST TREES

2. PINUS STROBUS L.

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Object and scope of the investigation

(WITH PLATES XIII AND XIV AND TWO GRAPHS)

The present paper is the second of a series presenting the results of studies of growth in forest trees.¹ The investigations are planned with a twofold purpose, namely to clear up some disputed points regarding the formation of annual rings and to outline the laws of growth in trees. The results of the studies of *Pinus Strobis* L. are presented in this paper.

Pinus Strobis L. (white or Weymouth pine) was chosen for the second subject of investigation for several important reasons. First, it is a soft pine and differs from the hard pines, which include *Pinus rigida* Mill., both in external as well as internal anatomy. Further, it is more rapid in its growth than pitch pine, and interesting results were anticipated from a comparative study of the two trees. Finally, white pine is of recognized commercial importance, and it is hoped that some of the conclusions will prove of interest and value to foresters.

The specimens in the investigations, aside from the seedlings, were all in the wild state. The investigations were not limited to a few trees or to one locality. Specimens were examined in different woodlots, thereby providing variation in site, soil, and other silvicultural conditions. Seedlings from the nursery beds of the Department of Forestry, N.Y. State College of Agriculture, Cornell University, small trees from the same, as well as others in the wild state, and older trees which had passed the century mark and presented wide variation in crown development, were all subjected to examination. Fully 50 specimens were studied and from them comparative data were secured. It is hoped that the results thus obtained will prove of permanent value in formulating general

¹ The first paper appeared in BOT. GAZ. 54:386-403. 1912, and included the investigations upon *Pinus rigida* Mill.

rules of growth for the species. Inasmuch as a description of all the trees used would be confusing, short silvicultural notes on each specimen will be given in the text where it seems necessary.

Previous investigations of growth in forest trees

Before entering upon a description of the methods employed in this work, a brief résumé of those of other investigators will perhaps add interest to the present study.

VON MOHL (25) sought to determine the growth of trees by making measurements of the circumference at a definite place on the bole. From these the radius was computed and the increase in thickness noted. CHRISTISON (5) pursued the same method and computed data for a large number of species, including both hard and soft woods. The data of JOST (13) were based in part on the methods given above and in part on measurements which he obtained by the use of a "Fuhlhebel."² Any data secured through bark measurement are unreliable because of continual changes going on in the older parts of the secondary cortex and changes which bear no relation to the newly forming rings. As a result, only broad generalizations can be drawn from data based on such methods.

T. HARTIG (12) sought to determine the growth of tree species in a different manner. Choosing even-aged, pure stands, where growth conditions appeared to be similar, he felled typical specimens from these at different periods and made comparative studies. He assumed that in such stands all individuals exhibited similar characteristics of growth, a view that is untenable in the light of our present knowledge. HARTIG'S method is open to criticism in that it was extremely inaccurate and could therefore never give reliable results. Growth varies markedly not only in different individuals in a stand, but also in different parts of the ring at a given height.

MISCHKE (24) took the first steps in the direction of securing accurate results. Using an increment borer, he studied the annual ring at different periods in its development and obtained in this way the first results which were in any way accurate. WIELER (39)

² For description see reference.

also followed this method and made many consecutive borings on coniferous and broad-leaved trees. His observations led him to infer that growth is very irregular not only as between different trees, but at different places in the same tree. The last named method, however, is subject to errors, and the results of WIELER show wherein it is inaccurate. When a boring is made with Pressler's increment borer, it is impossible to avoid applying some pressure to the wood core which is to be removed. During rapid growth (fig. 4) the elements of the newly formed xylem are thin-walled and easily crushed and displaced by pressure, however slight. The partially formed ring when treated in this manner may easily show a wide variability in diameter and thus lead to grossly erroneous results. This appears in part to explain why WIELER inferred that in neighboring areas growth varies considerably. I have already pointed out (1) that slight differences occur in neighboring areas, and the present investigation leads to the same conclusion, but the marked discrepancies in growth which WIELER describes are not present in either of the pines which have been examined.

Histological technique

The methods pursued were in general those followed in 1910. The technique, however, has been improved as the time and place to secure the best material became more evident with increasing experience. The chief objection is that it is necessary to make rather large wounds on the trees. This objection is not so serious, however, in coniferous trees because the resin which exudes prevents quite efficiently the drying out of the tissues.

The investigations on white pine began in August 1912, and continued until October 1913. Incisions were made on trees at intervals from base to crown (as high as it was safe to go in tall trees). Unless otherwise stated, these were always on the south side of the tree. A few cuttings were made on the north side for comparative purposes. Cuttings from branches at intervals were also made, and, unless stated otherwise, were lateral on the branch. Each cutting included all or a portion of the inner bark, the cambium, and all of the preceding year's ring except toward the end

of the season, when the growth of the years had attained such thickness as to make this impracticable. Duplicate cuttings were made on several trees at intervals of time varying from a few days to several weeks. These were always near the former cuttings and lateral to them. Rarely were the duplicate cuttings more than a few inches from the original ones. One series began in August 1912 and continued into September of the following year, cuttings being taken at least every month.

The material, as soon as obtained, was properly labeled and fixed in Gilson's fixer of the usual strength. Then after thorough washing it was run up through the lower grades of alcohol and stored in 65 per cent alcohol until wanted. The above corresponds to the methods used in 1910.

From this point the procedure varied depending on the object in view. When it was desirable to know the extent to which growth had progressed, or the abundance of starchy material present, freehand sections were made with a sharp razor. These were dyed with temporary stains and then studied. The HCl-phloroglucin stain for lignin, followed by the permanent Haidenhain's iron-hematoxylin stain for cellulose, gave excellent results. With this combination the extent of growth could be measured and estimated with accuracy. Chlor-zinc-iodide, as well as various combinations of I-KI, were occasionally used.

For minute examination of the tissues greater care was taken in manipulation. The material was demineralized with hydrofluoric acid and imbedded in celloidin. Sections were obtained in this manner 10-15 μ thin, which served the purposes of the investigation. Extensive and comparative histological studies were then made and the results tabulated.

The method described above makes it possible to follow the progress of the growth. One obstacle which could not be overcome was the inaccessibility of all parts of standing trees. In order to check up the results obtained, several trees of different ages were felled during the growing season. Accurate stem analyses were made of these and the progress of growth was observed throughout the tree. These data were then compared with those obtained from standing trees.

Investigations on the roots of trees were attempted and gave some results worth noting. The roots were secured from young trees (about 30 years). Other root studies were made on seedlings from the nursery. A few cuttings were taken from the roots of old trees where they were exposed near the base of the bole.

Microscopical characters of the xylem

The xylem of white pine is so well known that it is unnecessary to describe it here. When contrasted with the wood of pitch pine, the xylem of white pine differs in a number of anatomical features. The upper and lower walls of the ray tracheids are smooth as compared with the dentate ones of *Pinus rigida*. Bordered pits occur on the tangential walls of the late wood, while they are lacking apparently in pitch pine. The transition between early and late wood is not so abrupt in white pine and the rings are generally wider. White pine is a more thrifty tree, and the present observations tend to show that it is more susceptible to changes of site, soil, etc., than pitch pine. This is exceedingly important from the economic standpoint.

The roots of white pine exhibit the usual features of the roots of Abietineae. Diarch, triarch, and tetrarch roots are common. The root of seedlings is usually diarch (fig. 8), but the number of xylem rays is as a rule soon increased to three or four.³ Vigorous roots from thrifty trees between 15 and 30 years of age were pre- vailingly tetrarch, so that it would appear as if the number of xylem rays is correlated in some way with the amount of moisture available to the root and to the root environment, whether favorable or otherwise. VAN TIEGHEM (34) has noted this same variability in *Pinus*, *Abies*, and other allied genera, and further has pointed out that no constant relation prevails between the number of xylem rays and the number of cotyledons. Not only does the number of xylem rays vary in roots of different ages, but the number may increase or decrease during the growing season. This is strong evidence that environmental conditions influence within

³ Each xylem ray is terminated centrifugally by a resin canal, and the oligarchy of young roots can in this way be easily determined in cross-section with the naked eye.

certain limits the number of xylem rays. In general the larger the diameter of a yearling root, the greater the number of rays up to four. A pentarch or hexarch arrangement was not observed in any case, although it may occur, since VAN TIEGHEM (*op. cit.* p. 7) reports the number as high as 7 in Scotch pine (*P. silvestris*).

The xylem in old roots is comparable to that in the aerial parts of the tree, but differs in several well known particulars. The tracheids in roots have wider lumina and thinner walls and are never as well lignified as those in the parts above ground. This is especially well seen in cross-sections. In roots late wood formation is not as pronounced, owing no doubt to a decrease in mechanical strain in underground parts. The bordered pits on the tracheid walls, in both roots and stems, are mainly radially arranged. The uniseriate arrangement is here and there interrupted by the pairing of some pits. Further, the bordered pits in roots are larger than in the xylem of aerial parts. It is of interest to note in this connection that wherever an old root becomes exposed it usually presents xylem typical of aerial parts, so that only underground parts exhibit the characteristics above described.⁴

Winter condition of secondary cortex and cambium⁵

The secondary cortex of white pine is very similar to that of pitch pine. It presents the same radial arrangement of the elements, this arrangement becoming less regular as they are pushed to the outside (fig. 1). Companion cells are totally lacking, but one distinct row and a few scattered bast parenchyma cells are formed each year as in pitch pine, and these indicate the annual phloem areas in the old cortex. Occasionally the phloem parenchyma becomes crystallogenous, but never attains the size of that of pitch pine. The marked differences which exist between the bark of white pine and pitch pine are not present in the young phloem, but are caused by changes which take place subsequently in the outer cortex.

⁴ KNY (20) has pointed out the same structure in *P. silvestris*, and found that it was especially pronounced on the underside of large roots which had been exposed through erosion.

⁵ The notes only include observations on the winter condition of aerial parts, as underground parts were not accessible at this time of the year.

The resting cambium as seen in cross-section consists of 2-10 layers of tabular cells lying just outside the last formed xylem elements. SANIO and other early anatomists considered the cambium as consisting of a single initial layer, which through repeated division gave off daughter cells centripetally and centrifugally. These divided a second time, and the resulting cells enlarged and became elements of the phloem or xylem. The initial layer, if present in white pine, cannot be distinguished as such. The cells in each layer of the merismatic tissue are similar to the others in size, form, and protoplasmic content. The number of layers of cells in the cambium apparently varies between rather wide limits. Such variability might lead one to think that the work was not accurately done. The figures given above are as exact as the material permitted. The cambium is a very variable tissue both in number of cell layers and thickness of the same. Data indicating this (table A) were computed from measurements on tree I, a description of which follows.

Tree I was a thrifty specimen of white pine standing near the edge of a mixed stand on the brow of an incline which sloped northward into Six Mile Creek valley. The height of the tree was 55 feet, and crown development extended to within 18 feet of the ground. The tree was directly exposed to the south. Ground cover included sparse brush and pronounced sod formation. Cuttings were first made on this tree in August 1912, at heights of 4, 17, 30, and 43 feet from the ground, and were repeated at frequent intervals until September 1913, as recorded in the tables. Twig cuttings from near the top of the crown were also taken from time to time. The data in the table are from the cuttings of February 20, 1913.

TABLE A

WINTER CONDITION OF CAMBIUM, TREE I

Cutting	Thickness of cambium	Cell rows in cambium	Average width of last formed rings
2 year twig.....	5-9 μ	2-4	691.0 μ
6 year twig.....	5-9	2-4	661.0
12 ft. from apex.....	29-31	6-7	3367.0
25 ft. from apex.....	32-40	7-9	4297.6
38 ft. from apex.....	29-35	7-10	3013.8
51 ft. from apex.....	29-35	7-9	2894.0

It follows from the table that in white pine trees which are growing rapidly, the cambium is smallest both in number of cells and thickness in the smaller twigs and branches. It increases gradually in thickness and number of cell layers until that point is reached in the bole where diameter growth is a maximum. The decrease in the figures indicating the dimensions of the cambium are not proportional thereafter with the decrease in growth in diameter. It would appear as if the cambial layer, once it had attained its largest proportions, varied little in vigorous trees. In suppressed trees, however, it may reasonably be assumed that the cambial layers fall off in number and thickness toward the base of the shaft, but in such cases the reduction is not closely correlated with decrease in the width of the completed annual ring.

Another point relating to the cambial and phloem tissues deserves description here. I refer to the statement commonly made in textbooks that while the formation of xylem ceases early, the cambium continues to form phloem as long as climatic conditions are favorable. It is of interest to note in this connection the condition of the young phloem and cambium on September 26, 1912, and February 22, 1913. In all four cuttings of the first named date we find the condition as shown in fig. 7. Xylem formation had apparently ceased, the cell walls in the last row of tracheids were still in the process of thickening, but no new elements were being added. In the phloem we find a broad band of sieve tubes with a few parenchyma cells interspersed among them, making up in all some 15 rows of cells. This represents, with the possible addition of two or three rows of partly crushed elements to the outside, the seasonal growth of phloem. It is to be noted here that none or very little compression had occurred.

Comparing the above with what occurred on February 20, 1913 (figs. 2 and 3), the following interesting changes are to be found. Contraction had taken place, due to low temperatures during the winter, but not all of the sieve tubes are flattened to the same extent. In each of the four cuttings of February 22, the 3-5 last formed sieve tubes are only partially distorted by pressure, and those in the higher cutting (fig. 2) noticeably more so than in the lower cutting (fig. 3). In the last case there is a sharp dividing

line between the compressed sieve tubes and those which exhibit no compression. Further, as will be shown subsequently, the latter are the first sieve tubes to function the following spring. We may say that in white pine phloem development continues longer than xylem development. It only ceases with the extreme cold temperatures of December and January, and the tree makes no special provision for cessation of growth as in the xylem. Sieve tubes in all stages of arrested development may be found during the dormant period.

General discussion of tree growth

Growth as it occurs in trees falls logically into two subdivisions: growth in length and growth in thickness. In the first category we have only primary growth. It does not matter whether elongation is going on in root, stem, or leaf, it always has its inception in a growing point, and all tissues resulting from cell divisions in this apical meristem are primary tissues. Growth in thickness, on the other hand, results mainly from secondary thickening which is brought about through the activities of a perennial cambium. Tissues arising in this way are distinguished as secondary tissues in contrast to primary tissues.

The primary tissues, with the exception of the primary cortex, usually soon attain their full size in both coniferous and dicotyledonous trees, and in the majority of woody plants we may regard them, with the one exception mentioned, as mature at the end of the first growing season.⁶ Secondary growth, however, commonly begins the first year, and as a result the processes of primary and secondary thickening overlap, and both often go on at the same time in closely neighboring parts of the tree. Secondary thickening may thus occasion alterations before all the primary tissues have reached the adult state. It is entirely conceivable, for example, that both categories of growth go on simultaneously in the terminal shoot of a pine or in a young root. In this connection URSPRUNG (35) reports in certain cases the subsequent enlargement of the pith after secondary thickening had begun, so without

⁶ It is only in woody monocotyledons and tree ferns that primary growth persists for any length of time.

doubt these two processes overlap. For the sake of clearness in the subsequent discussion, however, growth in length will be considered in the general sense of primary growth, growth in thickness as secondary growth.

Awakening of secondary growth in aerial parts⁷

The awakening of secondary growth in aerial parts is first manifested in the cambium and the adjacent phloem tissue. It is evident in all cases several weeks before actual cell division begins. The cambial cells and last formed sieve tubes (6-10) open out radially, so that they attain several times their former diameter. Reference to the following table will show the changes which occurred between February 22, 1913 and March 29, 1913, in the width of cambium and last formed phloem.

TABLE B

GROWTH WITHOUT CELL DIVISION, TREE I

Cutting	February 22, 1913	March 29, 1913	Per cent increase	April 12, 1913	Per cent increase
I.....	69.0 μ	91.5 μ	32.6	113.3 μ	49.7
II.....	89.1	110.6	24.0	182.9	105.3
III.....	94.1	140.7	70.0	180.4	81.0
IV.....	103.3	171.1	56.0	188.5	82.0

In all cases, enlargement of the tissues in question occurred between the first two dates, and amounted from over a quarter to nearly three-quarters of their original size. The place of greatest enlargement was in cutting III, 17 feet from the ground. This does not correspond with the place of greatest ring thickening (table A) the previous year. Whether any significance can be attached to this discrepancy cannot be decided with certainty. It seems reasonable, however, to ascribe it to heightened temperature from the rise of soil water in the xylem.⁸ It would be natural to assume

⁷ No observations have been made on secondary growth in the leaves. MEISSNER (21) has observed a marked increase in the number of phloem elements and a very slight increase in the xylem elements in a number of species of *Pinus*.

⁸ ROBT. HARTIG (11, p. 262) made note of the temperature of soil water as a factor potent in forwarding growth.

that the greatest increase would be in cutting II. However, as this was 30 feet above the ground, it is quite possible that the tissues there had not yet experienced the increase in temperature due to the rise of soil water in the trunk.

The present investigation gives no reliable data as to where the first phloem activity was manifest. It had occurred throughout the tree on March 29, 1913. The awakening of growth began in this one specimen before the first of April and was not accompanied by cell division. Soil water was apparently largely instrumental in its inception.

If we refer again to table B for the data for April 12, 1913, two weeks later, we may draw the following interesting conclusions. The greatest diameter increase at this time is in cutting II, where it has been over 100 per cent. In other words, the ascending soil water may have reached the point of greatest growth (because the previous year's ring was widest here) and caused a rapid expansion of the tissues. In cuttings III and IV we find an apparent reversal of the foregoing conditions. Cutting III has increased only 11 per cent during the same period, while in cutting IV we find the increase has been 26 per cent. This may be ascribed to two causes, either one or both of which may be responsible. While the increased temperatures may have prevailed longer in IV than in III, the amount of reserve food material available was not as great. As a result, growth in cutting IV may have been retarded more than it was in cutting III; or cell division may have occurred in some of the cuttings and upset the equilibrium. Careful counts were made to find the number of cells in the cambium and last formed phloem in all four cuttings of March 29 and April 12. While slight differences occurred, these were not such as to warrant the conclusion that cell division had taken place between the two dates. The changes which occurred between March 29 and April 12 were due solely to enlargement of cells already present. We must infer then that the apparent contradictions of the figures in table B are due to differences of available food in different parts of the tree.

Cell division had begun in tree I by April 26. At this time the activity was manifest in cutting I (table C). Here some 8-12 tracheids and 2 or 3 new sieve tubes were already formed. Wall

thickening had not begun in the new tracheids, but was noticeable in the first of the new sieve tubes. Cutting II exhibited only slight evidences of cell division, while in cutting III growth was well started. No division had yet occurred in cutting IV. Growth had been very rapid in cuttings I and III, as evinced by the absence of thickening of the cell wall. This may be accounted for in part by the high temperatures which prevailed between April 22 and 26. During that period the mean daily temperatures ranged from 52° to 70° F. Precipitation amounted to only 0.03 inch, but large amounts of ground water were available at that season.

TABLE C

BEGINNING OF GROWTH BY CELL DIVISION, TREE I, APRIL 26, 1913

Cutting	Growth	Number of tracheids	Wall thickening	New sieve tubes
I.....	Present	8-12	None	2-3
II.....	Indication	0-1	None	0-1
III.....	Present	6-9	None	1-2(?)
IV.....	None	0	None	0

To explain plausibly the conditions in cutting II, the point of greatest growth the preceding season (table H), is not an easy task. Every indication seems to show that we might expect most rapid growth at this point. We can conclude only that the restricted growth here denotes one of the many idiosyncrasies of tree growth, where, as pointed out by WIELER (38), marked differences may occur in closely neighboring spots. It is to be expected that growth would not be manifest in cutting IV at this early date, so we may conclude that in tree I cell division was in evidence on April 26 in the upper portion of the bole but had not yet begun at the base.

In order to check the results on tree I, four bole cuttings, including the terminal leader and four branch cuttings, were made on a neighboring tree on May 4, 1913, eight days later. Tree II stood about 10 feet from tree I, and was apparently of the same age and subject to the same silvicultural conditions. The extent of growth and lignification in this individual is given in table D.

It follows from table D that on May 4 cell division was going on in all parts of the bole on the south side of the tree, with the exception of the terminal leader. It was farthest advanced in cuttings II and III, as might be expected, because the last formed annual ring was thicker here than in the basal cutting.

TABLE D

EXTENT OF GROWTH IN TREE II, MAY 4, 1913

Cutting	Number of tracheids	Amount of lignification	Remarks
I. Terminal leader, 1 year's growth.....	None	None	Phloem active; no cell division
I. Same, 2 years' growth....	1-2	None	Same as above
II. 44 feet above ground ...	12-15	1-3 tracheids	New phloem elements. cell division
III. 33 feet above ground ..	12-15	1-2 tracheids	Same as above
IV. 5 feet above ground....	10-12	None	Same as above

The branch cuttings were made on a branch which ran out some 20 feet in a southeasterly direction at a distance of 13 feet above the ground. Five cuttings were taken at intervals of about 4 feet. In cutting I (beginning from the tip) no tracheid formation was evident. In cuttings II and III tracheid formation was in progress, while in IV and V (basal) enlargement of the tissues had occurred, but no cell division. Cell division in the branches was similar to that in the bole, but more sluggish. It begins back of the branch leader and is most tardy in the base and leader of the branch. Which of the last is the first to exhibit growth depends on the length and vigor of the branch.

Numerous other observations were made on trees of different ages and different localities. It was found that cell division may be in progress some time in the upper portions of a tree while it is totally lacking below. This applies especially in old mature trees in closed stands, where growth is proceeding very slowly. Further, in general cell division first begins on the south side of the tree and in the basal portions. This peculiarity, due apparently to insolation, has also been observed in some cases in pitch pine (1).

It was noted in reviewing the literature on tree growth, that some (14) have attempted to correlate growth awakening with

the opening of the buds and the formation of new leaves. With this point in view, measurements were made on a young white pine stand of natural origin on May 3, 1913. The trees varied in age from 4 to 11 years and were in a thrifty, vigorous condition. On this date the buds were found to have opened and the young stems to have elongated 0.5-2.5 inches. All the growth in length had occurred in the preceding 10 days. Neighboring trees which were older showed less pronounced elongation of young parts; but growth had been in evidence in older, less favored trees since March 29, 1913, and cell division at least since April 20 of the same year. It follows, therefore, that growth in thickness begins before growth in length, and apparently, at the start at least, at the cost of reserve food material. No correlation exists between the two in white pine.

Concerning the time of cambial awakening, the researches of others bear out the conclusions of this paper. Some of CHRISTISON'S (5) are given in table E. It should be noted, however, that CHRISTISON'S results were obtained from bark measurements and do not necessarily indicate xylem formation.

TABLE E

GROWTH AWAKENING IN CONIFEROUS SPECIES, EDINBURGH, SCOTLAND

No. of tree	Name	Year	Awakening of growth
8.....	<i>Abies Lowiana</i>	1890	April 6
92.....	<i>Abies Lowiana</i>	1888	April 16-30
66.....	<i>Abies Douglasii</i>	1890	April 20
6.....	<i>Abies Douglasii</i>	1888	April 16-30
91.....	<i>Abies</i>	1890	April 13
2.....	<i>Pinus excelsa</i>	1890	April 6
26.....	<i>Pinus Pinaster</i>	1890	May 3
39.....	<i>Cedrus africana</i>	1888	April 16-30

MISCHKE (24) also made observations on this point, but did not include white pine among the species investigated. WIELER (39), however, examined three white pines in his experiments of 1894. Two of these were from a closed 40 year old stand, the third a 15 year old tree from another stand, all near Dresden, Germany. Growth was in evidence in the younger specimen to the extent of 13 or 14 tracheids on April 24. No growth occurred at the base of

the others until after the first of May, but growth must have been in evidence in the higher portions of the tree before that date. In the latitude of Dresden growth apparently starts fully as early as at Ithaca.

Intensity of growth in aerial parts

As already noted, growth continues some time before cell division occurs. It is first manifest through the enlargement of tissues already formed during the previous year. When cell division begins, it proceeds at first very rapidly, and in such a way that more elements are added to the inside of the cambium than to the outside. This was plainly observed in the sections and included in the data in table C. There 8–12 tracheids have been formed, as compared with 2 or 3 new sieve tubes. The cells thrown off to the outside gradually become transformed into sieve tubes, or more rarely into phloem parenchyma cells. This is accomplished in the first case through a thickening of the cell wall and the formation of lateral sieve plates. The phloem parenchyma cells thicken their walls very little at first, but enlarge for several seasons and eventually attain a much larger size than the sieve tubes. In the outer bark their walls are often strongly lignified.

Evidence of the rapidity of xylem formation is readily obtainable in early May. It is not uncommon to find 10–15 tracheids fully formed (fig. 5) without any indication of thickening of the wall. Subsequently the thickening begins, and before it has progressed to any extent lignification is evident in the cell walls, as brought out by the phloroglucin-HCl reaction. Wall thickening and lignification never start, however, until tracheids have attained their maximum dimensions as seen in cross-section.

The rapidity of vernal growth in white pine is apparently contingent on three factors: (*a*) the amount of reserve food material, (*b*) moisture, and (*c*) temperature. The first is always at its optimum in the spring, as the abundance of starch in the storage tissues testifies. Moisture likewise, at this time of the year, is available long before the buds begin to open. GOFF (8) has pointed out the early resumption of growth in the roots of coniferous plants, and observations on white pine coincide with his results. The

first two factors, therefore, may be eliminated from the discussion because both are at an optimum in the spring.

The temperature of the cambial layer depends, on the other hand, on three factors: (*a*) temperature of the air, (*b*) temperature of the soil water, and (*c*) direct insolation. Which of the three is most potent in the awakening and rapidity of cell division has not been determined, because they are so closely related to each other. It would appear that the temperature of the soil water plays a prominent part in the awakening of growth because of the opening out of the phloem first near the base of the tree. Factors (*a*) and (*c*) would be entirely negligible here, or at least play a minor part because of the thick layers of bark. Growth in the spring begins before factors (*a*) and (*c*) could have reached any appreciable height, so that the heat derived from soil water is certainly potential in awakening growth.

It is quite impossible to separate factors (*a*) and (*c*) and to note their effect in all trees. However, cuttings secured from the north and south sides of isolated trees at the same height often afford ample evidence of the effect of insolation.⁹ Data were secured to bear out the foregoing statement as early as May 10, 1913. The tree examined was a "Wolf" white pine on the south side of Fall Creek beyond Forest Home, N.Y., a suburb of Ithaca. The specimen was 51 feet high, with a diameter breast height of 15.3 inches, and exhibited vigorous growth in spite of the poor soil conditions. At the date mentioned, tracheid formation had proceeded on the south side to the extent of 12-14 tracheids, while on the north side 9 or 10 tracheids had been formed. Lignification had not as yet set in, although all but the last 3 or 4 tracheids formed had apparently attained their ultimate size. That direct insolation is potent in the awakening of growth in trees is certain. However, one individual will present occasionally conditions the reverse of what would be expected.

It follows from the preceding paragraph that the awakening and the rapidity of growth depends on three factors, two of which are at an optimum in the spring and may therefore be neglected.

⁹ Trees should be selected only from sites which are level, as trees growing on slopes are subjected to other factors which often overshadow the effect of insolation.

The third (temperature) is a variable one, and to this the rapidity of cell division is apparently directly proportional. Some idea of the rapidity with which the formation of tracheids may go on may be drawn from the following. Basal cuttings were taken from the south side of the "Wolf" tree already described on May 3 and May 10, 1913. The first cutting showed no evidence of formation of tracheids, while the other, taken a week later, exhibited 7 tracheids in each row, complete as to size, with several smaller ones in process of formation. The growth in places farther up the stem must have been going on still more rapidly. While the period mentioned above was warm and humid and therefore especially conducive to rapid growth, it may be safely assumed that in all white pine trees in the vicinity of Ithaca formation of tracheids is very rapid at the start. A large number may be formed in a relatively short time.

Intensity of growth in aerial parts

In the discussion which follows, the distinction between intensity of growth and amount of growth must be kept clearly in mind. The latter may be easily ascertained for the whole growing season or for any part thereof by measuring at a given period the amount of new tissue. Growth intensity, on the other hand, is constantly changing. It may vary from week to week, day to day, and even within one and the same day, as FRIEDRICH has pointed out (7). The amount of growth during a given period is then the sum of the prevailing growth intensities multiplied by the time each was in force. Let us take a specific example. Suppose a white pine first begins the formation of new xylem on May 1, and, on May 30, 60 new tracheids were in evidence in each tracheid row. It does not follow that 20 tracheids were formed the first 10 days, and 20 during each succeeding 10 days, making a total of 60. While the average growth intensity was two tracheids per day, the actual growth intensity may have vacillated on either side of this amount. It is obvious that it is quite impossible through comparative studies to obtain the prevailing growth intensity at a certain definite time. In order to do this the growth process would have to be actually observed. Some idea of the variability in growth intensity may be

gained, however, by comparing the average growth intensities for different periods in the growing season. It follows that the shorter the intervening time periods, the greater would be the vacillations in the data. With this idea in view table F was constructed. It includes figures of growth intensity from tree I during the summer of 1913. The width in microns of the new growth is given for 6 different periods, together with the total increase from period to period and the average gain per day. The last will give, not the actual, but the average intensity of growth of the period just preceding.

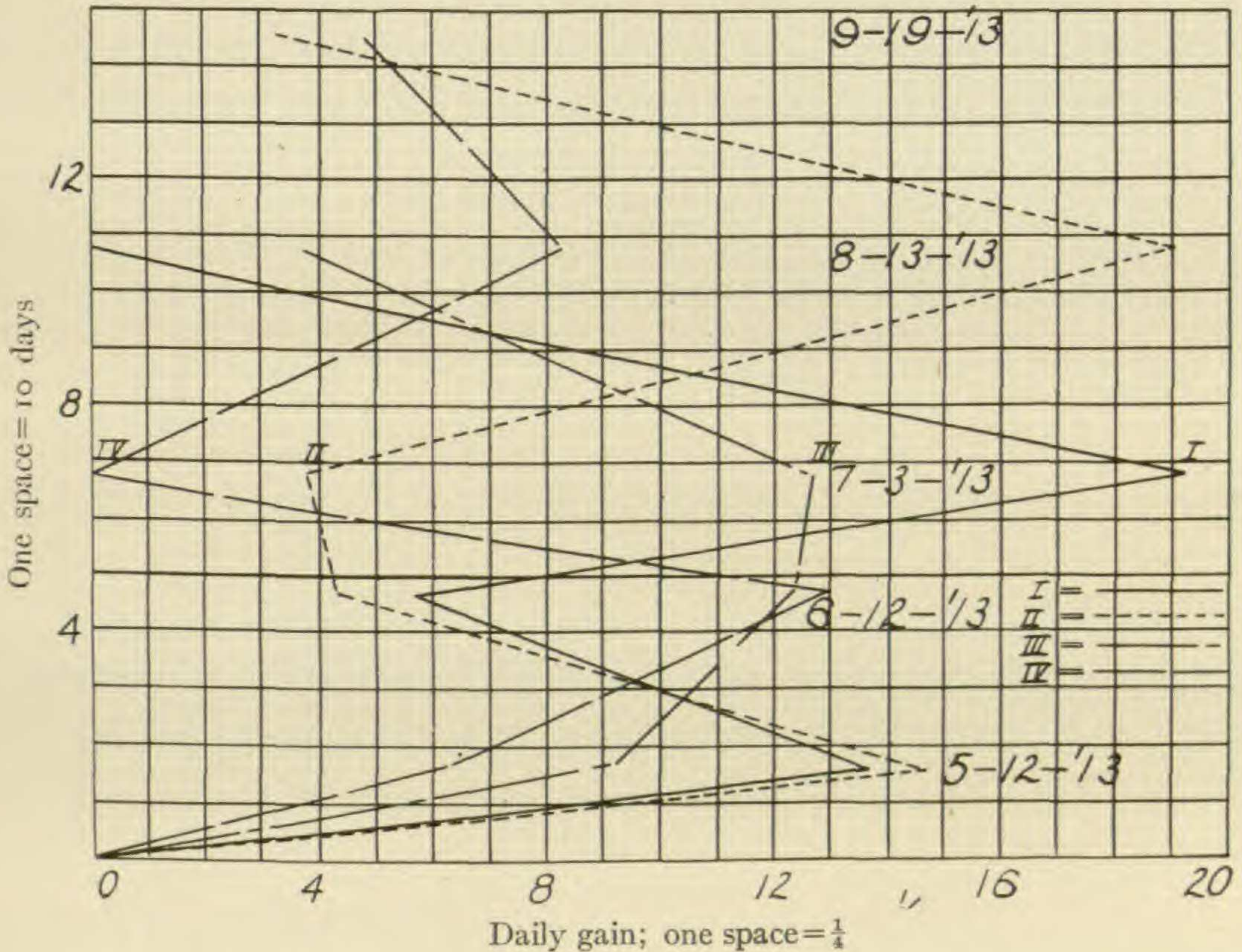
If the data of April 26 and May 12 are compared, the following points are to be observed. The average growth intensity was greatest in cutting II, with cuttings I, III, and IV following in the order named. On June 12, 31 days later, cutting IV exhibited the greatest average growth intensity, with cuttings III, I, and II following in the order named. Again, in the cuttings of August 18 and September 19, different combinations occur. At the first named date, growth was more rapid in cutting II, while at the latter date it was in cutting IV.

TABLE F

GROWTH AMOUNT AND INTENSITY, TREE I; SEASON 1913

No.	Amount 4-26-'13	No. of days	Gain	Gain per day	Amount 5-12-'13	No. of days	Gain	Gain per day
1.....	170.0 μ	716.3 μ	16	546.3 μ	34.1 μ
2.....	26.6	609.6	16	583.0	36.5
3.....	106.7	472.4	16	365.7	22.9
4.....	0.0	243.8	16	243.8	15.2
	6-12-'13				7-3-'13			
1.....	1164.2 μ	31	447.9 μ	14.4 μ	2176.0 μ	21	1011.8 μ	48.2 μ
2.....	1021.1	31	411.5	13.3	1224.0	21	202.9	9.7
3.....	1414.3	31	941.9	30.4	2067.2	21	652.9	31.9
4.....	1251.2	31	1007.4	32.5	1219.2	21
	8-13-'13				9-19-'13			
1.....	2176.0 μ	41	0.0 μ	0.0 μ	2176.0 μ	37	0.0 μ	0.0 μ
2.....	3100.8	41	1876.8	47.5	3394.6	37	293.8	7.94
3.....	2448.0	41	380.8	9.3	2339.2	37
4.....	2067.2	41	848.0	20.7	2502.4	37	435.2	11.8

The results given in table F are represented in graph 1. The abscissas indicate the daily gain and the ordinates the time intervening in 10 day periods. From the way in which the lines cross and recross, it is evident that average growth intensity and the actual amount of growth which is correlated with it vary between wide limits during different periods. The cambium may be very active for a time, then slacken in its growth, this to be followed again by renewed activity, with a final slump toward the end of



GRAPH 1.—Curves of growth intensity, tree I, 1913

the growing season. All the cuttings represent these two fluctuations except cutting III, and this departure may be accounted for through the inequalities of growth in closely neighboring parts.

Two periodic optimums of growth intensity have already been noted by others. FRIEDRICH (7) made observations with the help of calipers, and found that in both coniferous and hardwood trees there were two periods of growth, one lasting until the end of May, then sinking some until the middle of June, followed later

by another maximum again in July, and then rapidly diminishing and ceasing altogether. JOST (13) has carried on observations which substantiate those of FRIEDRICH. It is remarkable how well the deductions of these two investigations are brought out in graph 1.

The first optimum is without doubt made at the expense of the reserve food supply. It is not until June and even later that the bulk of the seasonal results of metabolism in the leaves is available. This causes the second optimum, which may occur in July or August. It might be said in this connection that the amount of moisture and the prevailing temperature has been responsible for the results in table G. The meteorological data which follow

TABLE G

METEOROLOGICAL DATA, SEASON 1913

Month	Mean temperature	Precip. in 0.01 in.	Month	Mean temperature	Precip. in 0.01 in.
April.....	48.1	1.49	July.....	70.4	1.59
May.....	55.4	3.15	August.....	69.6	1.92
June.....	65.0	2.00	September.....	61.0	3.28

are the best refutation of that argument. The decline occurred in three cuttings between the middle of May and the third of July, yet the temperatures prevailing were not such as to warrant this, nor was there a noticeable decline in the precipitation. My observations agree with those of FRIEDRICH, that there are in white pine at least two periods of maximum growth.

Irregularity of secondary growth in aerial parts

A thorough treatment of the increase in growth in trees must necessarily be very comprehensive. The study in all its phases is a comparative one, for only by resorting to comparison can any fundamental rules of tree growth be formulated. A comprehensive study should therefore treat comparatively of the growth of (a) one individual during one growing season, (b) of one individual from season to season, (c) of different individuals in the same stand during one season, and finally (d) of different individuals not in the same stand. Data bearing on the first, second, and last phases of the

subject are available. For the third the reader is referred to the publications of WIELER (37-39), JOST (13-15), R. AND T. HARTIG (9-12), MISCHKE (24), and others.

The amount of seasonal growth in an individual or of growth up to a given point in the season is equal to the sum of the products of the different prevailing growth intensities by the time each was in operation. It follows that these summations would be quite different in different parts of the tree. The only reliable method to indicate the amount of seasonal growth at a given point and at a given time is as a percentage of the previous year's ring. Even this is open to criticism, in that the annual increment often varies between wide limits from year to year. Yet general deductions may be drawn from data of this kind which will indicate to some extent at least the amount of growth at definite times. Table H was made with this idea in view. The figures were obtained from tree I. The width of the previous year's ring represents the average of the last formed rings as exhibited in the 6 different cuttings.¹⁰

TABLE H

AMOUNT OF GROWTH IN PERCENTAGE OF PREVIOUS YEAR'S RING, TREE I

No.	4-26-'13	5-12-'13	6-12-'13	7-3-'13	8-13-'13	9-19-'13	Average width preceding ring
I.....	3.8	16.0	26.0	48.7	4471.7 μ
II.....	0.7	17.2	28.9	34.6	87.7	96.0	3535.3
III.....	4.8	18.0	50.2	78.9	93.5	89.3	2619.4
IV.....	0.0	11.8	60.4	58.8	99.7	2071.7

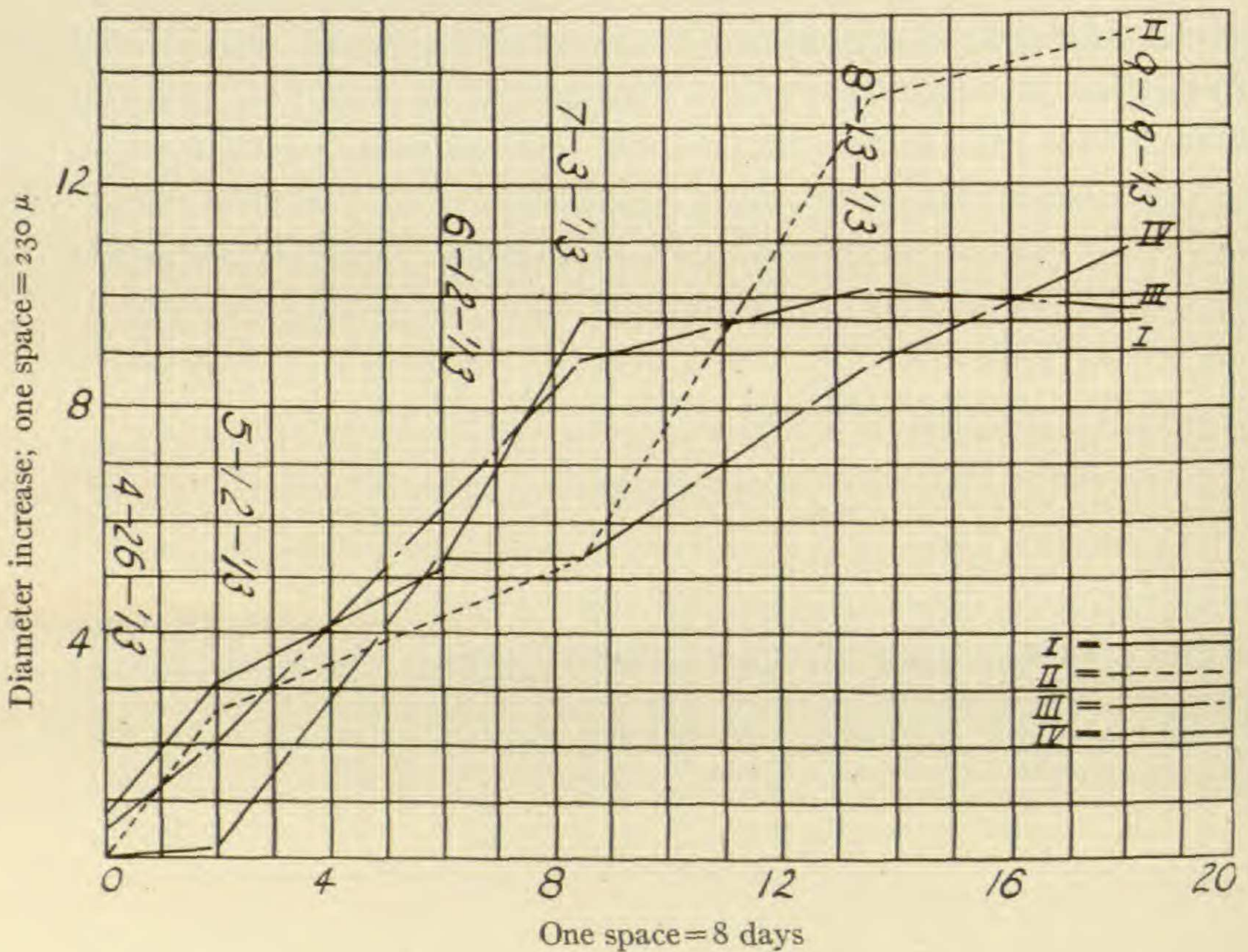
On April 26 the greatest proportion of new growth occurred in cutting III, with cuttings I, II, and IV following in the order named. On May 12 the order remained the same except that cuttings I and II had interchanged. On June 12 the ring was, theoretically at least, from one-fourth to over one-half complete; on July 3 from one-third to over two-thirds complete; while on August 13 seasonal growth was over four-fifths complete in all cases.¹¹ After the last named date, the growth was very sluggish

¹⁰ The last acts as a control and tends to eliminate error.

¹¹ Growth ceased in cutting I after July 3, 1913; see table F.

for the next 37 days. Though still in evidence at the end of that time, we may infer that the ring was to all purposes complete.

The contents of table H are presented in graph 2, where the abscissas represent the diameter increase of new growth and the ordinates 8 day periods. It is to be seen from both the table and the curves that in the long run the cambium in all parts of the tree tends to even up irregularities which arise from different growth intensities. If growth is sluggish at one place in the bole and rapid



GRAPH 2.—Curves of growth amount, tree I, 1913

in another during a given period, the pendulum of growth intensity swings to the other extreme in the next period and evens up the disparity.

The irregularities of growth are manifested not only in the actual dimensions of the new formed tissues, but in the number of new xylem elements as well. If careful average counts of new formed tracheids are made, and these compared with the average number of tracheids at that point in the preceding ring, irregularities

crop out all along the bole of the tree. The data given in table I illustrate this very well. They were computed from tree III on June 17, 1913. This tree was a vigorous specimen on the north end of a small island in Fall Creek, east of Forest Home. The height was 81 feet, the diameter breast height 21.5 inches,¹² and the age about 80 years. Exposure was to the southeast. Crown development was good but one-sided, and greatest to the southeast. Root development was also uneven, but the reverse of crown development, because the constant washing of the water and the mechanical action of ice had destroyed the root system on the east side. The tree was felled on June 17, 1913, and a double series of

TABLE I

EXTENT OF GROWTH IN TREE III, JUNE 17, 1913

CUTTING	N.W. SIDE		PERCENTAGE	S.E. SIDE		PERCENTAGE
	Tracheids in old ring	Tracheids in new ring		Tracheids in old ring	Tracheids in new ring	
I.....	55-65	20-25	0.38	55-65	20-25	0.38
II.....	32-34	15-18	0.52	30-35	15-17	0.48
III.....	22-24	9-11	0.43	30	18-20	0.63
IV.....	23-25	10-12	0.46	22	17	0.77
V.....	16-18	6-8	0.41	19-21	13-15	0.70
VI.....	16-18	6-7	0.35	23-25	14-15	0.63
VII.....	15-16	7-10	0.60	12-14	9-10	0.69
VIII.....	12-14	7-9	0.61	9-12	6-8	0.64
IX.....	12-14	5-7	0.46	12-14	7-9	0.62

9 cuttings taken at intervals of 10 feet, one on the northwest side and one on the southeast side (exposed). Careful average counts were then made of the number of new formed tracheids, as well as those in the preceding ring at each point. On June 17, 1913, growth was more advanced in every cutting on the southeast side, the first two cuttings excepted, than on the northwest side. This was to be expected, because of direct insolation and larger crown to the southeast. But in both series of cuttings marked vacillations in growth are evident, so that it follows that growth irregularities express themselves not only in a variability in thickness of tissue, but also in the number of elements laid down.

¹² Exceptionally high because of the buttressed base.

Growth irregularities in individuals have been noted by others, although their results are in some cases to be questioned because they were based on external measurements alone. Such are those of CHRISTISON (5), VON MOHL (25), and JOST (13), reference to whose work has already been made. The results of TH. HARTIG (12) and ROBT. HARTIG (10) can have no significance in this connection, inasmuch as individuals were felled to secure data and consecutive measurements were quite impossible. MISCHKE (24), as already noted, employed an increment borer, and his results, with those of WIELER (39) who pursued the same method, are more reliable though not as accurate as is desirable. The former made comparative notes on Norway spruce and Scotch pine, and his results clearly indicate growth fluctuations. WIELER subjected

TABLE J

GROWTH OF WHITE PINE AT DRESDEN, GERMANY

Date 1894	I		II		III	
	Ring breadth mm.	No. of tracheids	Ring breadth mm.	No. of tracheids	Ring breadth mm.	No. of tracheids
April 24	0.48	13-14
May 5	1.12	26
May 16	0.08	3-4	0.14	8-10	2.34	47
May 26	Lost	Several	2.00	47-50
June 5	0.11	3-4	0.18-0.20	4-6	4.12	89
June 16	0.06	2-4	0.12	6-9	3.15	72
June 26	0.15	6-8	0.16	6-8	2.74	73
July 7	0.19	8-9	0.46	15	5.61	113
July 17	0.45	15-17	0.47	13-16	6.67	150
July 28	0.23	8-11	0.53	20-23	9.23	175
August 7	0.42	17-18	0.32	15	6.25	150
August 18	0.34	12-18	0.31	14	5.68	135
August 28	15-20	0.30	13-15	5.22	119
September 8	0.26	11-13	0.55	23	9.32	218
October 17	0.38	13-19	0.38	16
November 1	0.26	11-13	0.49	20-22	9.26	212

more trees to the same inquiry, and his investigations are of greater interest because he worked on white pine. Table J indicates his results on the three different specimens mentioned previously, and in each case fluctuations in growth are marked. The work of BUCKHOUT (2) serves to accentuate the same point. He made bark measurements on a white pine and a larch which extended over a

period of 4 years. The results were plotted in curves where the abscissas represented 5 day periods and the ordinates increase in circumference in sixteenths of an inch. In each of the four curves for white pine, from several to many growth fluctuations are evident. Still other researches could be cited to emphasize the same point. Many irregularities in growth occur during the season of cambial activity.

Comparative growth studies between different individuals of white pine (not in the same stand) were also carried on during the summer of 1913. In such investigations only temporary mounts were made and the necessary data secured from these. A few extracts from this part of the work follow.

On May 10 two cuttings were made at the base of the "Wolf" tree previously described, one on the north side and one on the south side. The first exhibited about 10 tracheids (7 complete) as to size on this date, while 12-14 tracheids were in evidence on the south side. On May 9 two cuttings were secured from a large white pine which presented different conditions of site, although in the same vicinity. This was a mature specimen some 110 feet high and 22 inches diameter breast height. It stood in a mixed hardwood stand where the land sloped sharply to the south. Ground cover was sparse. The tree, while mature, appeared to be still in vigorous growth. The north cutting (next to the bank) exhibited 2 tracheids, neither complete as to size; while in the south cutting no new tracheids were to be seen. Without doubt growth was going on vigorously in the upper part of the tree at this date. Observations on the same tree at a later date showed similar discrepancies. On June 13 the south basal cutting of the "Wolf" tree showed 20-25 tracheids already formed; 15 or 16 of these had apparently attained their ultimate size. The same cutting from the older specimen at that date possessed 11-13 new tracheids, 7-9 of which had attained approximately their maximum size. The amount of growth was decidedly less in the older individual.

Even wider discrepancies may be expected than the above where the differences in age are greater. For example, a young tree was examined on the same date (June 13). This was a thrifty

14 year old individual situated in the midst of the stand and only a few feet from the "Wolf" tree. In fact, the "Wolf" tree may have been one of the seed trees from which the stand had arisen. The cutting was made at approximately breast height, and already on June 13 the annual ring exhibited some 90 new tracheids. Three weeks later summer wood formation began. It follows that up to July 1, at least, we may expect many discrepancies in growth to occur. The greater the difference in vigor between the two trees compared, the greater will be the difference in the amount of growth at that period.

Others have noted the same growth irregularities between different individuals of the same species. Among these is ROBT. HARTIG (10), who expresses himself emphatically on this point. I quote from his text as follows:

Bei freiem Stande und directer Insolation des Baumes, besonders aber des unbedeckten Bodens beginnt der Zuwachs in den unteren Stammtheilen weit früher, als im geschlossenen Bestande und bei einem Boden, der entweder beschattet (Nadelholzstand) oder von einer dichten Humusdecke bekleidet ist. An 100 jährigen Fichten, welche isolirt an einem Südhange standen, war schon am 1. Mai auf Brusthöhe der Dickenzuwachs in Thätigkeit, an ebenfalls frei stehenden gleich starken Bäumen des Nordhanges auf nasskaltem Boden war am 26. Mai noch kein Zuwachs bemerkbar. Im vollen Waldesschlusse zeigten manche Fichten und Kiefern selbst am 1. Juni noch ruhendes Cambium auf Brusthöhe, u.s.w.

An excellent illustration is likewise afforded by WIELER's table (table I). Trees I and II were in a 40 year stand, where they had been subjected to similar silvicultural conditions. WIELER failed to say whether tree II was bored on the north or south side, but in either case the tracheid numbers are seen to be quite different from those in tree I. Growth curves from neighboring trees under similar conditions never coincide. Fluctuations are constantly arising which upset the regularity of growth and for which no one factor is responsible.

Termination of secondary growth in aerial growth

The autumn condition of the cambium was observed in tree I both in 1912 and 1913, inasmuch as cuttings first began on this tree on August 5, 1912. The data given in table K include the

results obtained from two cuttings in 1912 and the last two cuttings of 1913. The table is of value because it offers comparative data which are strongly correlated with the results of others. While the periods of time between the cuttings of 1912 and 1913 are different, it is obvious that in each year the greatest increase of xylem toward the end of the growing season was in the basal cutting. In other words, growth continued vigorously at the base of the shaft until well into September, while in the higher parts it had either

TABLE K
TERMINATION OF GROWTH, TREE I; 1912 AND 1913

CUTTING	WIDTH OF RING		AMOUNT OF INCREASE	PERCENTAGE OF INCREASE	NO. OF DAYS	PERCENTAGE OF DAILY INCREASE
	Aug. 5, 1912	Sept. 26, 1912				
I.....	2643.8 μ	3176.9 μ	533.1 μ	20	52	0.38
II.....	3046.4	52
III.....	2529.6	2622.1	92.5	3.6	52	0.07
IV.....	1550.4	2328.3	777.9	50	52	0.96
	Aug. 13, 1913	Sept. 13, 1913				
I.....	2176.0 μ	2176.0 μ	31
II.....	3100.8	3394.6	293.8 μ	9.5	31	0.31
III.....	2448.0	2339.2	31
IV.....	2067.2	2502.4	435.2	21.1	31	0.68

totally ceased, as in cutting I, 1913, or continued very sluggishly,¹³ and this condition was exhibited by tree I during two successive years.

It follows from the preceding paragraph that in normal white pine trees growth is apparently first retarded above, retaining its vigor longest in the basal portions of the bole. The results of others on coniferous species lead to the same general conclusion. T. HARTIG (12) worked on both hard and soft wood trees and came to

¹³ The disparity in the data of cutting I for the two consecutive years may be questioned. In 1912 there was an apparent gain of 20 per cent during the period intervening between the two dates given, while in 1913 no growth was evident at all after the first date. But in 1912, the first cutting was made on August 5, while the following year it was 8 days later. This probably accounts for the increase in the first case. Growth was still in evidence there on August 5, but had the cutting been made 8 days later, the results might have been decidedly different.

the conclusion that cessation of growth occurred later below and last of all in underground parts. R. HARTIG (11), following up these studies, made cuttings from species of *Pinus*, *Picea*, *Larix*, and *Abies*, in order to determine the condition of the cambium in different parts of the shaft. Cambial activity in each case was farther advanced above than below. It gradually diminished in intensity during the months of May, June, and July in the higher parts, while below the same applied to the months of June, July, and August. KNUDSON'S data (16) indicate the same condition of the tissue for *Larix laricina*, except that in the larch the phenomenon occurred in July instead of August and September.

The disparity in growth in different parts of a tree is without doubt dependent on conditions of temperature. The primary cortex persists in white pine for a long period, in some cases as long as 50 years. This condition is brought about through the division of the original cells of the cortex by anticlinal walls, and the subsequent enlargement of the two cells thus resulting. Meanwhile, cork formation remains superficial, so that the upper portions of the tree, even where the bole is 15 inches in diameter, are clothed by a layer of living, chlorophyll-bearing, primary cortex. Sooner or later, however, and varying markedly in different individuals, deep cork formation begins. This is evident first through the formation of isolated areas of brown tissue which stand out sharply from the surrounding living cortex. These increase in number, finally become confluent, and the characteristic old bark of white pine is formed. With this change in the type of cork formation there is correlated a modification of at least one factor potent in forwarding growth. The first phellogen is continuous around the whole circumference and functions until deep cork formation begins. New cork cells are added to the outside, and with the increase in circumference the older ones on the extreme outside slough off. So long as the primary cortex persists, the corky mantle remains thin and its protective value is in like proportion restricted. With deep cork formation, however, the conditions are altered to a large extent because the corky layers which are then formed through the activity of each phellogen accumulate. Protection of the cambium in the basal portions of the tree is thus greatly increased.

Changes in temperature are less effective there because the thick corky layers tend to equalize the conditions which prevail at different times during the growing season. Cool autumn nights, for example, would chill the cambium in the upper parts of the tree much earlier than below. Temperature changes become operative first where the primary cortex still persists, that is, where the bark is yet smooth. This without doubt explains the disparity of growth as we find it in white pine. Growth is first retarded above, but may go on vigorously below for a much longer period.

The exact time of growth cessation apparently varies widely in different species, in different localities, and in different sites. While wide variations occur, still certain generalizations apply. At the outset the term "growth" is a misnomer. As already noted, phloem formation, at least in conifers, does not cease with xylem formation, but continues uninterruptedly until late in the fall. It is necessary, therefore, to discuss xylem and phloem separately in their relation to cessation of growth.

A comparison of cuttings from tree I for the years 1912 and 1913 will give an idea of the seasonal termination of xylem formation. One discrepancy was noted at the start. In spite of the fact that the final cuttings in 1912 were a week later than those in the following year, growth was apparently more vigorous at the later date in 1912 in all four cuttings. This is to be explained in two ways. It was due either to seasonal variations or to the fact that the vigor of the tree had been materially lessened the second year through the many cuttings taken from it. An examination of the meteorological data for the two seasons has added no convincing evidence, inasmuch as comparative figures of growth for the two years were not at hand for a sufficiently large number of individuals, and general assumptions were therefore out of the question. Possibly both factors were in force.

To give the exact time or a definite place in the tree for the termination of xylem formation is quite impossible, as the data on tree I indicate (table F). In 1912 growth was still in evidence on September 26 in all four cuttings, as transitional forms of tracheids could be noted in every case (fig. 6). Growth, however, was going on at this date very sluggishly. Often only one flattened transitional

tracheid occurred between a cambial cell and a fully formed (as to size) tracheid, and occasionally here and there in a cutting this was lacking entirely. Again, in the cuttings of September 19 of the following year the same condition of affairs existed. While growth as to relative amount had to all purposes ceased, still all indications pointed to the fact that in all four cuttings it was going on, though very slowly. In both cases growth appeared to be most sluggish in cutting III, but no reason can be assigned to account for this fact.

The data from the preceding paragraph lead to the following conclusions. Xylem formation in tree I continued during two successive years until the last half of September, possibly even as late as October 1. Further, it was in evidence throughout a large part of the bole, as cutting I was 38 feet above the ground and the terminal leader extended only 17 feet beyond. Whether it still continued in the terminal leader cannot be concluded from the present investigation. If we correlate these deductions with those previously reached in the paper, the following points are evident: (a) growth intensity falls off first in the upper parts of normal white pine trees, more tardily below; (b) cessation of xylem formation does not follow the same law, but persists sluggishly in all parts of the bole (with the possible exception of the terminal leader) until the latter part of September; (c) the exact time of the end of xylem formation was not determined in the present investigation, but it is safe to conclude that it was practically complete by October 1.

The results of the present study are contrary to those of ROBT. HARTIG (9), who says, "Der Abschluss der Zuwachsthätigkeit erfolgt oben entsprechend früher, als unten." Too much emphasis must not be placed upon this statement, because (1) HARTIG made external measurements only, and (2) his results may have been influenced by subsequent phloem formation after xylem formation had ceased. ROBT. HARTIG avoids the issue in part when he states that cambial activity occurs in the tops of trees in *Pinus silvestris*, *Picea excelsa*, and *Larix decidua* during the months of May, June, and July, and at the base during June, July, and August. While he implies also a cessation of growth, he does not say it in so many

words. WIELER (39) has given some data concerning the termination of growth from the three white pines which he investigated (table J). In tree I the ring was complete on the north and south sides at the base on September 8. In tree II it was complete on the south side at the same height on August 28, while in tree III it was still in progress on September 8. In general his results indicate that in the vicinity of Dresden, Germany, growth in white pine ceases slightly earlier than at Ithaca, N.Y., a reasonable conclusion, since the former is in a higher latitude. The work of BUCKHOUT (2), already cited, is of interest in this connection. While his measurements were made externally and are therefore subject to the same criticisms as those of TH. HARTIG, certain facts are obvious. During the four years over which his experiments extended, growth was manifest in the white pine during the last 10 days in August and in two as late as September 8. His results serve to accentuate the fact that white pine has a long growing season, much longer than the European larch, with which he also worked.

The growing season of tree I may be used, in spite of variations which occur between individuals in that respect, as a general indicator of white pine growth in the vicinity of Ithaca. As already indicated, growth in white pine may be divided into two periods: (A) growth without cell division and (B) growth with cell division. B of necessity follows A. Considering A and B together, growth began in tree I before March 29, 1913, and continued until after September 19 of the same year, a period of over 5.5 months; and this does not include the late phloem development which without doubt continued into October. Cell division began before April 26 of the year in question, and if growth is considered in the narrow sense, the period is shorter by several weeks. If there are any grounds for the statement that trees complete their seasonal growth in a period of 4 or 5 weeks, white pine is an exception to the rule, as here the growing season extends over a period of 4-5 months, depending on the interpretation of the term "growth."

Differentiation in the annual ring in aerial parts

In working up the foregoing data, no stress has been laid on differentiation within one and the same annual ring. As is generally

known, each normal ring may be divided into spring wood and summer wood, or better early wood and late wood. The second of these two regions is distinguished from the first either by a diminution in the size of the vessels, as in the case of ring porous woods, or through a reduction in size and flattening of the elements formed in the outer part of the ring. The proportion of early and late wood in the ring affects strongly the physical properties of the wood, and as a result the early workers gave much time to its consideration. The factors controlling the amount as well as the time of late wood formation have been a subject of inquiry, and a hasty review of the literature on the subject, as well as a summary treatment of the results of this study from this viewpoint, are appropriate here.

One of the first theories offered to account for the variation in ring was that of KRAUS (19), SACHS (30), and DEVRIES (36), who explained it through differences in bark pressure at different times during the growing season. The radial pressure was at a minimum in the spring, permitting a greater expansion of the new elements, while it gradually increased during the growing season, ending with a maximum. The pressure leading up to the last was responsible for late wood formation. This theory was disproved by KRABBE (17, 18) beyond all contention in 1882, and since that time a number of new theories have sprung into existence, each with adherents.

ROBT. HARTIG (9) sought to explain the late wood formation in that the cambium was but poorly nourished in the spring. Late wood formation depended upon improvement in the nutritive conditions later in the season. According to HARTIG the size of the lumina of tracheids is dependent on the amount of transpiration of the foliage, while the thickening of cell walls is correlated with the increased amounts of food available at that time of the year. Diametrically opposed to HARTIG's theory is that of WIELER (37) and RUSSOW (29), which was based on the assumption that the early wood owed its origin to better conditions of nourishment.

STRASBURGER (32) accepts neither of these theories, but explains annual ring formation as a normal fixed process. The young wood is the response, according to his theory, on the part of the plant

to a demand for conducting tissue, while the late wood is formed to increase the stability of the tree. The last factor may have been in force from the beginning, but was at the start overshadowed by the first.

MER's theory (23) rests firmly on the general assumption of WIELER as given above. According to his idea, the early wood results when the cambial activity is at a maximum, that is, in the spring, while late wood formation occurs when growth is going on very sluggishly, as in August and September in the white pine. The last elements of the annual ring are flattened because with the falling off of growth intensity the radial stretching of the young elements subsides in the same proportion.

Still another theory is of interest here because it departs decidedly from all of those mentioned. SCHWARZ (31) assigns the chief rôle in late wood formation to longitudinal pressure. This is in force throughout the growing season, but its effects are lost at first as the result of other factors, such as nourishment, which are temporarily more potent at that time. With a decline in the action of these, the effect of longitudinal pressure (gravity) reasserts itself.

No attempt has been made in the present work to refute or substantiate any of the theories above mentioned, nor in fact to bring forward a new hypothesis for annual ring formation. Other workers of the last decade have given the matter serious thought, but the problem still remains unsolved. It is the opinion of the author that several factors are potential, but inasmuch as these cannot be controlled by the investigator, the precise influence of each on growth cannot be definitely determined. The results obtained appear to substantiate MER's theory to some extent, in that growth in tree I was more rapid in the spring and early summer than subsequently. But the assumption that the cambium was better nourished at the beginning of growth than later is not justified from the present inquiry. It can only be said, in conclusion, that late wood formation occurs at a time when growth is proceeding very slowly.

No definite results were obtained concerning the time that late wood formation begins. White pine does not lend itself to a study

of this sort, because the transition from early to late wood is always very gradual, and it is difficult to distinguish the first formation of late wood tracheids. Larch should prove much more satisfactory for this study. But in spite of the difficulties mentioned above, it was obvious that late wood formation was in evidence in tree I on August 5, 1912, and on August 13 of the following year. On each of these dates all four cuttings showed some traces of it, and, further, it appeared to be slightly more advanced in cuttings I and II than in the ones taken lower on the bole. This was to be expected from what has been previously said; late wood formation begins first in the upper portions of the bole.

Primary growth in aerial parts

Some attempt was made in the investigations to secure reliable data concerning the elongation of aerial parts. A sample plot of 0.05 acre was laid off on May 3, 1913, in the vigorous young white pine stand mentioned previously. It included 115 trees which ranged from 4 to 11 years. The soil was of medium thickness, underlaid by sandstone and shale; exposure was open. All the trees were seemingly vigorous.

The trees were first examined on May 3 as to elongation of aerial parts. At that date elongation had already begun in all the trees on the plot, which varied from 0.5 to 2.5 inches. Greatest elongation had occurred in the terminal leader, while it was less pronounced in the slower growing lateral branches. The leaf fascicles were in evidence, but had as yet attained no appreciable length.

Observations corresponding to the above were subsequently made on May 30, June 17, and July 4 of the same season. Accurate measurements of the terminal leader and of the preceding year's growth for 50 trees were made in each case and the results collected in table L. The average growth of the preceding season is considered as the mean of the average preceding year's growth as found on May 30, June 17, and July 4. It is to be observed that the last vary slightly, as no attempt was made to select the same 50 trees on each date. The measurements are given in inches and fractions of inches.

Elongation of aerial parts began in the young growth in question before May 3 and continued until about July 4. Assuming that growth before May 3 proceeded at the same rate as between May 3 and May 30 (1.2 per cent a day), we can only infer that the awakening of growth in length in the shoots began about 8 days before (April 25), a conclusion that field observation fully confirmed. Cessation of growth in length in shoots had occurred by July 4, without doubt because at this date the length of the season's growth had surpassed that of the preceding year, and furthermore the terminal cluster of buds was fully formed. It follows from the data that in 50 young trees in 1913 elongation of the terminal shoots

TABLE I
GROWTH IN LENGTH IN THE TERMINAL LEADER

Date	Average seasonal growth	Average growth of preceding season	Mean growth of preceding season	Per cent of preceding seasonal growth	No. of days	Per cent gain	Per cent gain per day
5-3-1913.....	1.25	13.55	9.3
5-30-1913.....	5.6	13.98	13.55	41.3	27	32.0	1.2
6-17-1913.....	10.02	13.22	13.55	73.9	18	32.6	1.8
7-4-1913.....	14.37	13.45	13.55	106.1	17	32.2	1.9

began in the last part of April and continued until July 4. What applies to the terminal shoot is even more applicable to the lateral branches where long growth is not as vigorous. Furthermore, the same relation exists between young and old trees. In the latter growth in length must have been completed by July 4, so that it may be concluded that in white pines in the vicinity of Ithaca, growth ceases during the early part of July.¹⁴

Before proceeding to a review of the results of others, perhaps a brief discussion of the elongation of the leaf is appropriate here. Only one observation was made in regard to this point, but fortunately the date was July 4, so that it offers a chance for comparison between growth of shoots and leaves. The leaves on the

¹⁴ MEISSNER (22) has noted the formation of the so-called "Johannistriebe" in rare cases in white pine. Bud formation occurs in the normal way, but in such cases some buds continue growth the same year. This peculiarity has been noted in many dicotyledonous fruit trees, but is rare in conifers.

terminal shoot of the season were compared with those of the preceding season as to length (not thickness), and the results tabulated in table M in inches. Only 6 trees were examined, so that we cannot expect the uniformity that more extended observations would offer; still, the results are of value in that they lead to a general conclusion.

TABLE M

TABLE OF LONG GROWTH IN NEEDLES

DATE	NEEDLE LENGTH		DIFFERENCE	GROWTH PERCENTAGE	AVERAGE GROWTH PERCENTAGE
	Old	New			
7-4-1913	3.75	2.38	137	63	63
7-4-1913	2.75	1.75	100	63	63
7-4-1913	2.88	2.00	88	69	63
7-4-1913	2.88	2.13	75	73	63
7-4-1913	2.75	1.13	62	41	63
7-4-1913	2.38	1.75	63	73	63

Elongation in the needles had not ceased on July 4; in no case was it three-fourths completed, as a reference to the table will show. Assuming that elongation in the needle is contemporaneous with elongation in the shoots,¹⁵ that is, that it began on April 26, it follows that during a period of 69 days the needles had attained on an average 63 per cent of the average growth of the preceding season. Assuming again that the rate of elongation was the same during the rest of the season, we may compute roughly the period necessary for the needles to complete their growth, that is, growth in length in the needles would be completed about 40 days after July 4, that is on August 13. It is reasonable to assume from the data on the 6 trees that the elongation of white pine needles ceases somewhere about the middle of August.

If we correlate the results given above with those which have been previously given, we arrive at the following interesting conclusions for white pine in the vicinity of Ithaca. Growth in thickness (secondary thickening) begins in white pine before the elongation of aerial parts, either of shoots or needles. Elongation of shoots and needles begins simultaneously. The elongation of

¹⁵ Field observation substantiated this assertion.

the shoots ceases during early July, while that of the needles continues well into August.

Comparative studies of the growth in length of shoots and needles have been made by others. WIELER (39) found, for example, that in the needles growth was completed in *Pinus montana* at the beginning of July, in *Pinus austriaca* at the end of August, in *Pinus silvestris* by the end of July and the beginning of August, in *Pinus Strobus* during the course of August. Growth of the needles in *Pinus*, according to his observations, varies with the species. MEISSNER (22) likewise noted that growth of needles of a number of species of pine varied, especially that of *Pinus silvestris*. While he gives no exact date for the termination of growth of needles in the species, he states that growth in length of the terminal shoot ceased about the middle of July, and in all cases the growth of the needles continued later than that of the shoot. Whether all species of *Pinus* agree in this respect remains yet to be determined; white pine has proved no exception to the rule.

Primary growth in underground parts

The detection of primary growth in underground parts is in some species attended with obstacles which are well nigh insurmountable. Often the new tissues are little or not at all differentiated from those of the preceding year, and in such cases it is very difficult to detect the beginning of growth in length in the spring. This is the case in white ash, where little coloration results, so that it is quite impossible to separate new and old parts of the root. Fortunately, in the Coniferae this does not apply, for within a space of 1 cm. marked brown coloration appears, so that new growth can be detected without any difficulty. Furthermore, after the cessation of growth in the autumn, this brown mantle approaches nearer the root tip, so near in fact that one can be reasonably sure as to the presence of new growth.

The first observations on root growth were made on April 26, 1913. Roots were obtained from 3 and 4 year white pine specimens in the nursery. The frost had been out of the upper soil layers for only a short time, yet evidences of growth were to be seen in many of the root tips in the shape of small white translucent

protuberences 1 mm. or so in length. Very little elongation had occurred, but clear evidences of its inception were to be seen. Growth in length had already begun.

This early study, as well as the subsequent ones, also brought out another interesting point in regard to white pine roots, namely that there are two kinds of roots underground, just as there are two kinds of branches above. This is well brought out in fig. 11, where long roots and short roots are plainly visible. The short roots occur irregularly on the sides of the long roots, either singly or in tufts of varying size. Where the latter occur, they arise through the forking of a normal short root; this is repeated a number of times and each branch remains short and acquires a growing point of its own. Occasionally one of the apices in the tuft grows out into a long root, but the majority of them remain short, function for a time, but eventually die and disappear as the diameter of the long root increases. Other workers have already noted the same condition in white pine roots. BÜSGEN (4) has described it in some detail, and adds further that mycorrhiza are found in the long roots, while they are entirely lacking in the short roots.

Data bearing on root growth were next obtained on May 10. Roots were taken from a thrifty young pine about 12 years old, which from its position on the north bank of Fall Creek near Varna, N.Y., was admirably fitted for the purpose in hand. The creek had partially undermined the sandy bank, and root apices were readily obtained by digging back into the bank. Some of these are represented in fig. 12. The new growth had already attained a length of two inches in many cases, and, as seen in the figure, was sharply marked off from that of the preceding year. This is due to the fact that in the last cork formation (as well as secondary thickening) had occurred, and the thick primary cortex which forms the bulk of the thickness in the new growth was entirely lacking. Browning of the tissues, a peculiarity already described, had also started in the new growth, as the root tip at the extreme right bears evidence. Lateral roots in the form of translucent dots were just appearing on the sides of the growth of the preceding season. It was quite impossible on May 10 to make comparative notes of root growth in 1912 and 1913, inasmuch as the point of origin of growth in the spring of 1912 was not evident. All trace

of yearly elongation is lost after the first year. No attempt was made to trace rapidity of growth of white pine roots. Roots from the same tree on May 30 exhibited an average growth of 4-5 inches, but no other material was secured. We can only infer from the data at hand that growth in length began as early as April 26, possibly much earlier.

The results of others in regard to the duration of root growth are interesting in this connection. RESA (27), after repeated observations on root growth, came to the conclusion that there are in all roots two periods of root development, one in the spring, which occurs mainly before the unfolding of the leaves, and a second during September and October. The last persisted through the winter in dicotyledons, with many interruptions from time to time, but without complete cessation. In conifers, on the other hand, there was a decided rest period during January and February. WIELER (38) combated RESA'S conclusions and maintained that in the autumn, after leaf fall and the resulting lessened demand for water, no new roots were necessary. PETERSON (26) worked with young and old trees of a number of dicotyledons, as well as specimens of *Picea excelsa*, *Pinus montana*, and *Larix decidua*. His results in every way substantiate those of RESA and contradict the conclusions of WIELER. Among other points explained, PETERSON points out that there is a period of root elongation which may occur in the spring anywhere between February and June. In June, and especially in July, elongation gradually ceases. This is followed by a reawakening in growth in length from August until October and even into November. The author does not state in which period growth is more intense. The researches of BÜSGEN in 1901 (4) and ENGLER in 1913 (6) substantiate in every way those of RESA and PETERSON, so it may be concluded that there are two periods of elongation, and furthermore, that in white pine the first begins in late April and continues into early June or even later.

Secondary growth in underground parts

Secondary growth in roots, as in stems, begins the first season, and once started proceeds in the usual way. Mention has already been made of the variability in white pine roots as regards the

number of xylem rays. The secondary xylem forms between the primary xylem rays and under the primary phloem, and it follows that there are as many secondary xylem areas as there are primary xylem rays. In a young root where the secondary thickening has begun we find the primary and secondary xylem areas alternating with each other (figs. 9 and 10). It is usually not until the following year that the segments unite and complete the ring of cambium.

An unsuccessful attempt was made to find out at just what period in the growing season secondary thickening began in the root. Roots were examined on May 11 and again on May 30 with this object in view. No secondary growth was in evidence in either case in the new tissues, even when, as at the last date, elongation had gone on to the extent of 5-6 inches. In every case, however, where the last formed growth of the preceding season was examined, secondary xylem was in evidence between the poles of the primary xylem, and evidence of a resting period was to be seen, so that it must be concluded that secondary growth occurs later in the growing season than May 30, probably during the second period of activity in the autumn. The cambial segments, however, apparently do not unite over the poles the first year, so that secondary growth the first season is confined to as many separate areas as there are poles.

The course of secondary thickening in the root, once started, is much more irregular than in the aerial parts. The annual rings are usually thickest on the lower side of the roots as they enter the root crown, but all regularity is lost a short distance from the bole. The rings may be narrow here and broad there, and apparently their position in the ground has no appreciable effect; geotropism is not a factor in annual ring formation. False and double annual rings are often present. As RUBNER (28) has pointed out, the cambium may be active on one side of a root and dormant on the other for several years without its vitality being impaired, and this is responsible, in part at least, for the irregularities in growth which arise. Furthermore, the tissues of exposed roots present the same characteristics as those in aerial parts, a peculiarity previously noted by KNY (20). In conclusion, it may be said that roots,

while conservative structures in many respects, exhibit much more irregularity in annual ring formation than do stems.

Summary

1. The winter condition of the secondary cortex and cambium of white pine is similar to that of *Pinus rigida*. The marked differences which occur between the mature bark of white pine and pitch pine are occasioned by changes which take place in the outer cortex (periderm).

2. The cambium varies both in number of cell layers (2-10) and thickness in different parts of a tree. It is smallest in both these respects in the twigs and young branches, and increases gradually in dimensions from the apex downward, until that point is reached in the bole where the last annual ring is the thickest. Thereafter, the decrease in the diameter is not proportional to the falling off in the diameter of the last formed ring.

3. Phloem development continues until late in the autumn, much longer than xylem development. Sieve tubes in all stages of formation occur between cambium and fully formed phloem. The seasonal growth of phloem exhibits little or no compression as late as October first. Subsequently contraction occurs, due to the extreme cold temperatures of winter. All the seasonal growth of phloem is crushed with the exception of the last 6 or 8 transitional tracheids. Compression is greater in the crown than below.

4. The processes of primary thickening and secondary thickening overlap, and both may be going on in closely neighboring spots in the tree at the same time.

5. Growth in white pine is divisible into (a) growth without cell division and (b) growth with cell division. The first begins as early as March and the elements concerned (phloem) increase in radial diameter from 50 to over 100 per cent. The awakening of growth is due apparently to the rise of soil water with an accompanying increase in temperature.

6. Growth by cell division begins during the last half of April. At the start it is very rapid, and more elements are formed at the inside of the cambium than at the outside. The formation of

new xylem elements follows the same order as in pitch pine, that is, it begins first in the bole at some distance below the apical shoot and spreads upward and downward. As a result, growth at the base of a tree may begin several weeks later than in the crown.

7. The awakening and rapidity of growth is dependent on three factors, moisture, available food (reserve), and temperature. The first two are at an optimum in the spring; the amount of growth therefore is directly proportional to prevailing temperatures.

8. The intensity of growth is a variable factor which changes from day to day and even within a single day. Two periodic optimums of growth intensity occur, one during May and early June, the second in July and August. These vary from time to time at a given height in the tree and follow no definite law.

9. The amount of growth at a definite time and place in the tree is equal to the sum of the prevailing growth intensities by the time each was in force. It is very irregular at different heights in the tree, but the cambium tends to even up discrepancies as the season progresses. The irregularities of growth are manifested not only in the actual dimensions of the newly formed tissues, but also in the xylem elements. Wide discrepancies may occur in closely neighboring trees; in general, larger differences may be expected the greater the disparity in age.

10. Growth is first retarded in the upper portions of the tree; it may continue vigorously below for some weeks longer.

11. Xylem formation goes on very sluggishly in all parts of the tree (the terminal leader excepted) until late September and early October, phloem development as long as temperature permits.

12. The total growth of white pine extends over a period of 5.5 months, growth by cell division between 4 and 5 months.

13. Late wood formation begins during the first half of August; it is associated with a decrease in growth intensity and begins first in the higher parts of the tree.

14. Elongation of new shoots and leaves is simultaneous and begins in early May; it manifests itself only after xylem formation has begun. Growth in length in the shoots ceases about July 1; needle growth may continue until August 15 or even later.

15. White pine has long roots and short roots. Only the first elongate to any extent and often are in symbiosis with mycorrhiza. Growth in length begins during the last half of April, in some cases even earlier; no reliable data were obtained regarding its cessation. Secondary growth occurs during the first season and proceeds in the usual way.

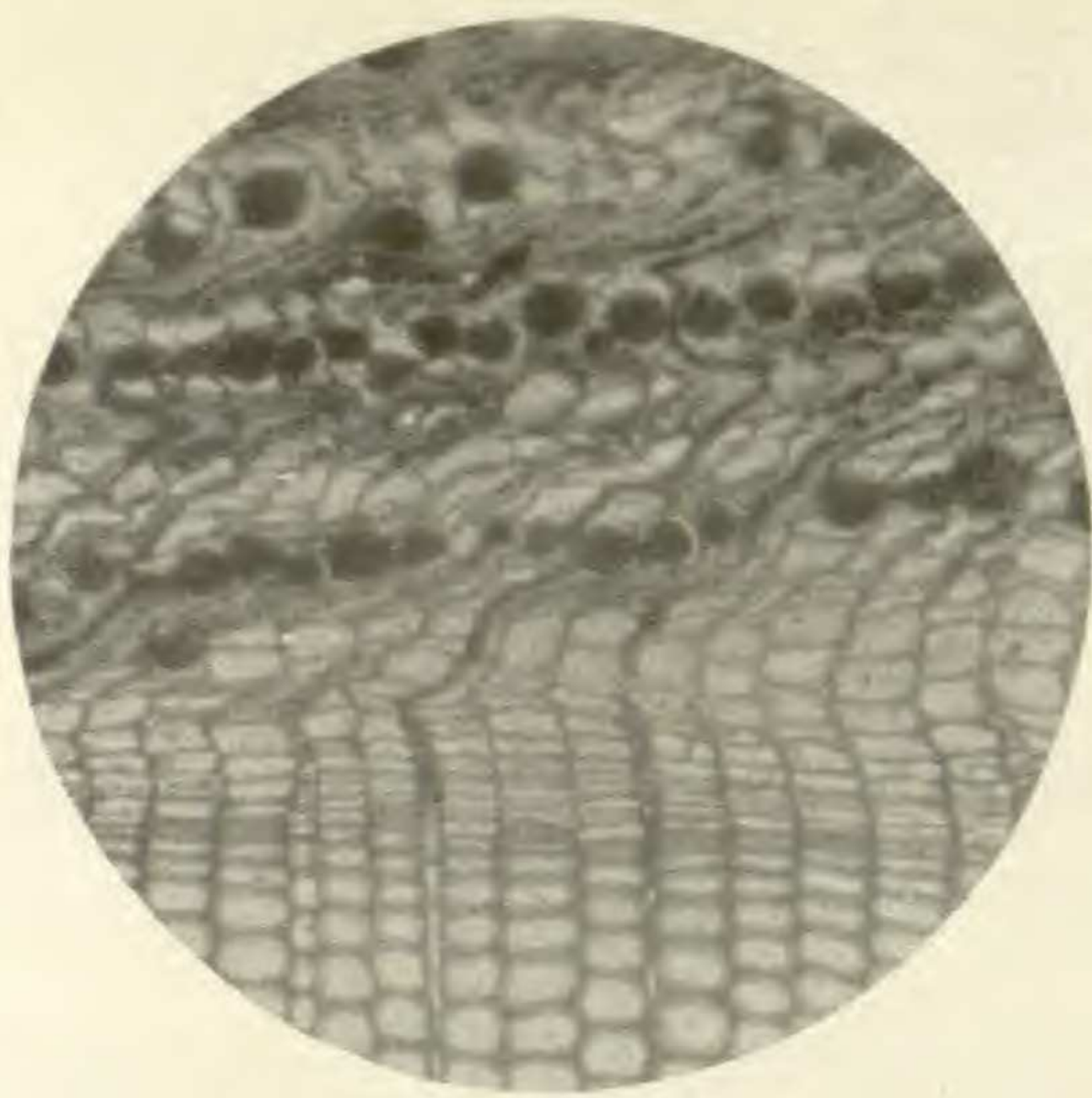
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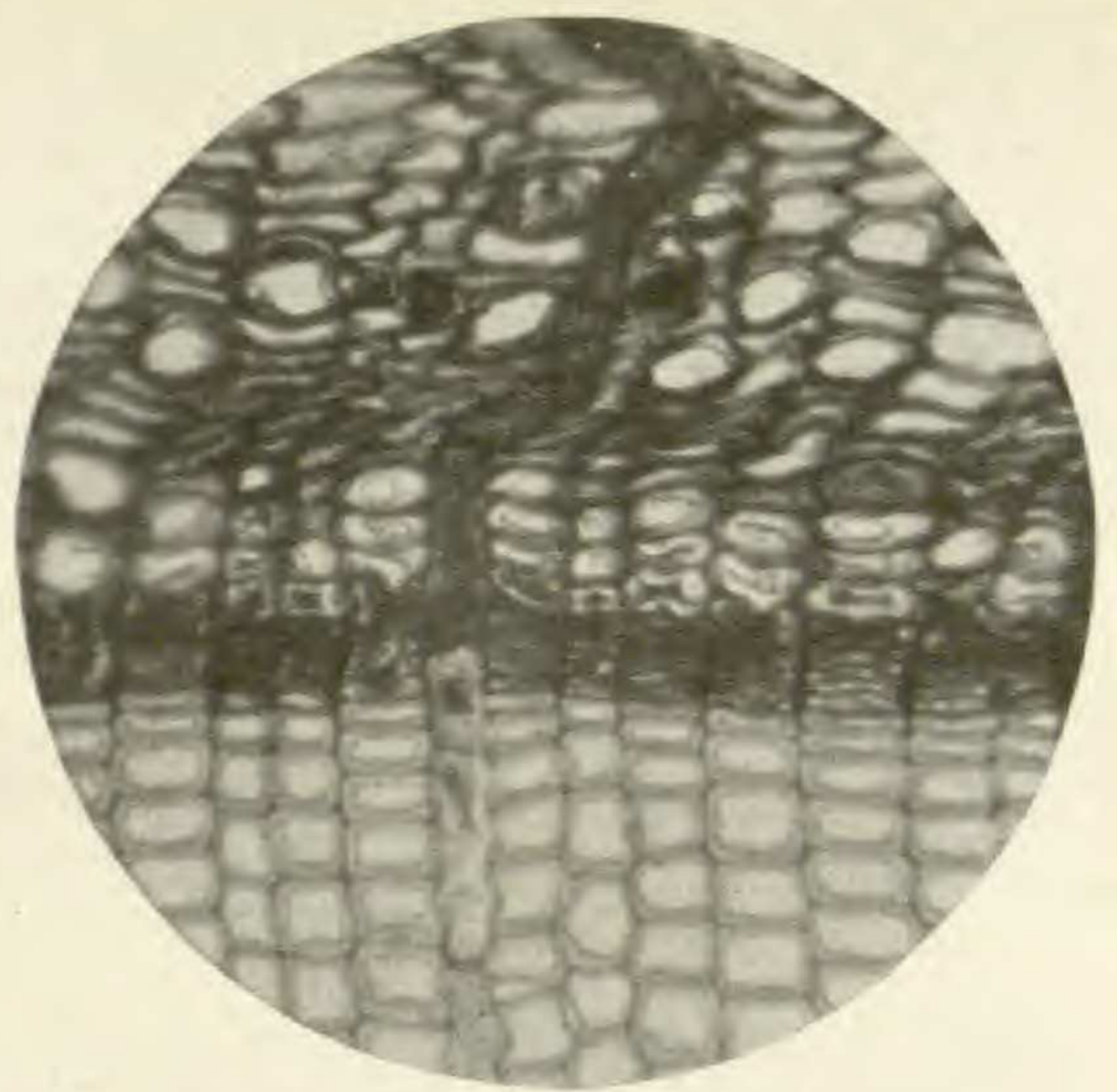
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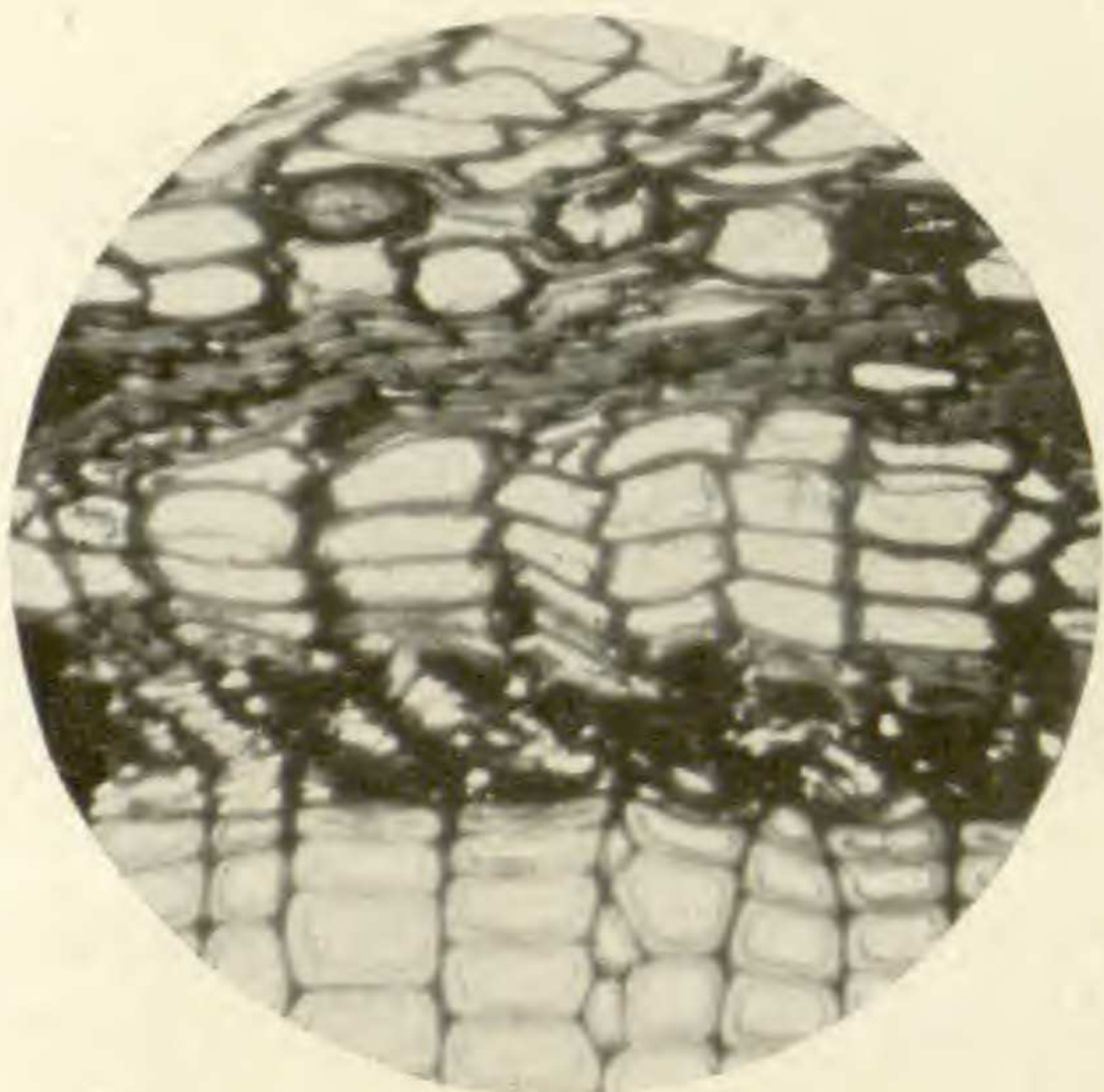
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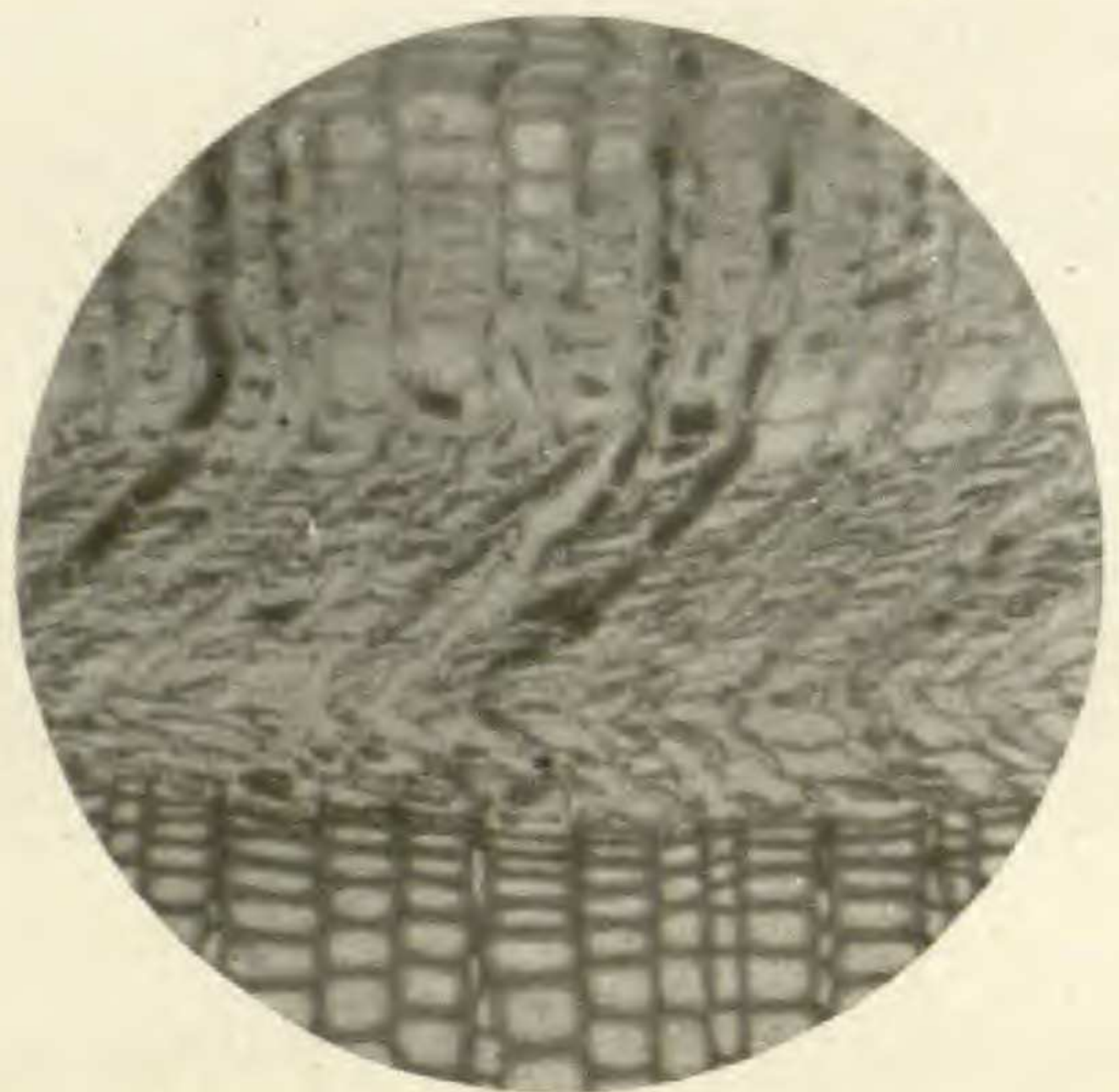
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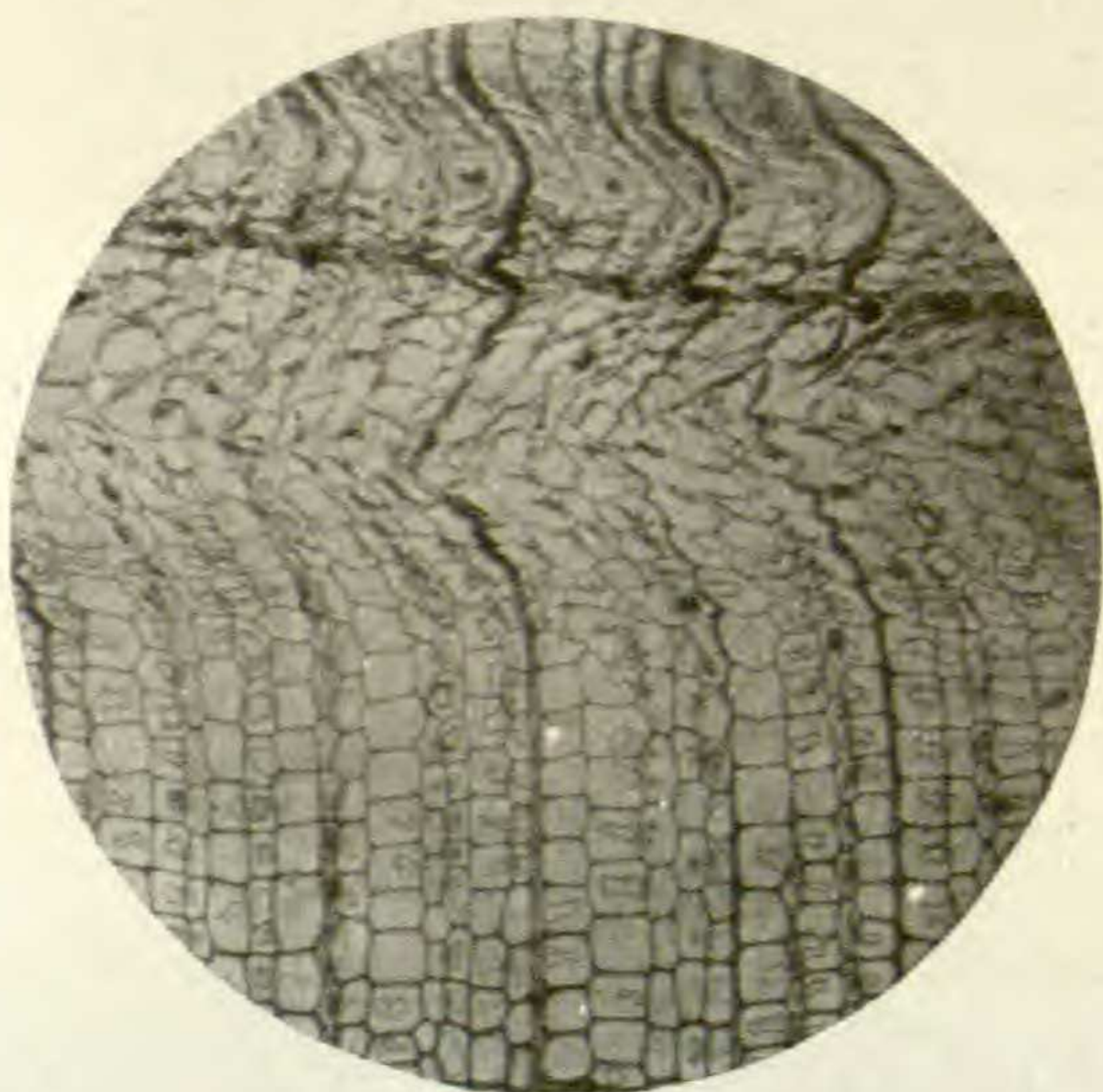
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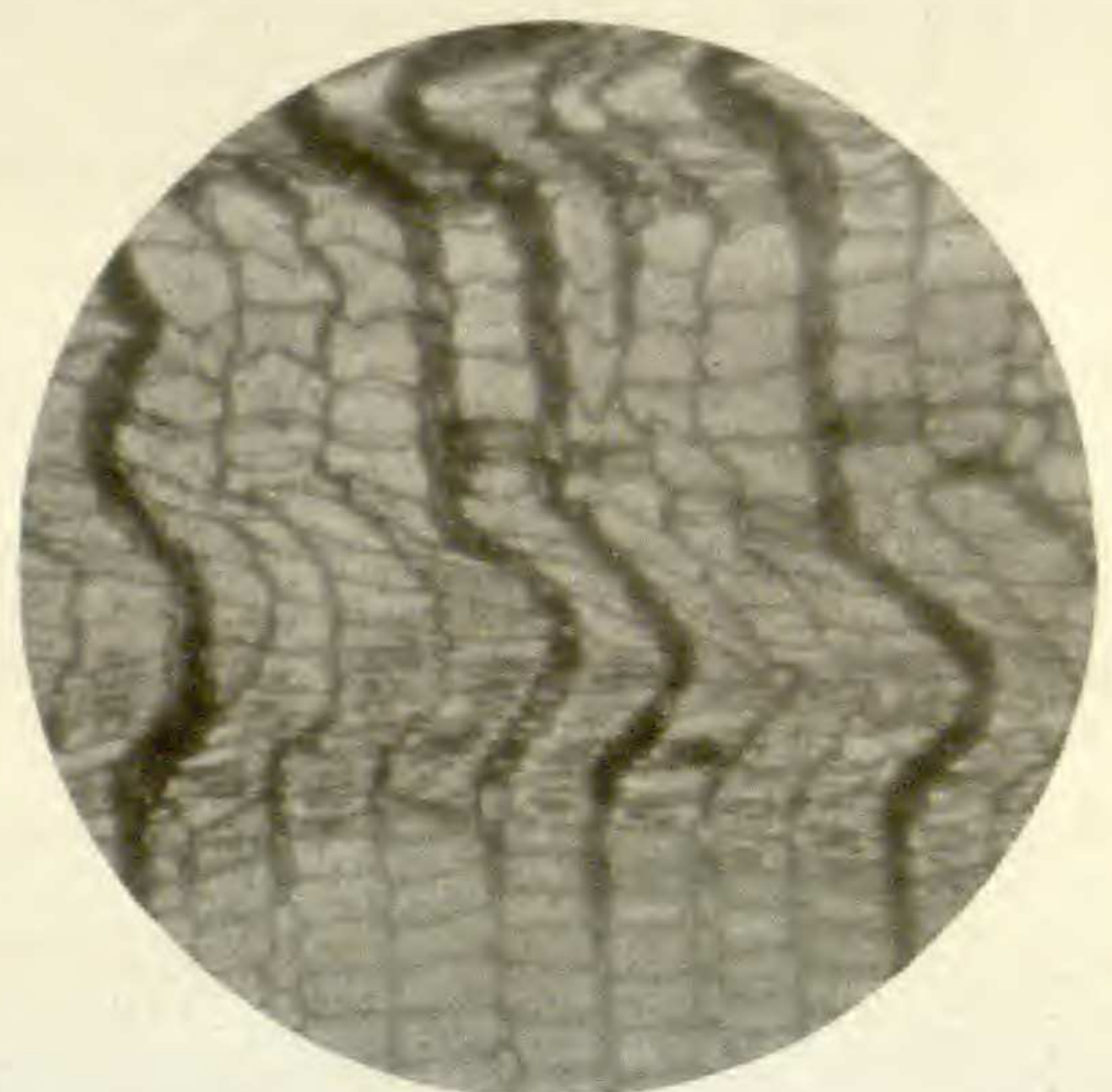
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BROWN on PINUS STROBUS